

TRIBAL REVISIONS IN THE ASTERACEAE. III.

A NEW TRIBE, LIABEAE

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Attempts to establish more natural concepts for the Compositae have revealed two genera, Liabum from the Senecioneae and Cacosmia from the Helenieae, which are very closely related to each other and which are rather remote from all other genera. The two genera are placed here in a new tribe having closest relationship to the Vernonieae.

The exclusively Western Hemisphere group of plants was noted first by Linneaus on the basis of a West Indian species under Amellus a genus of the tribe Astereae. Separate generic status was first established with the description of Liabum by Adanson in 1763. The first significant attempts to classify members of the group were those of Kunth and Cassini in the early 19th century. Kunth (1818) recognized Liabum under the new genus Andromachia and included the genus in his subsection Astereae of the section Carduaceae. The subsection included primarily genera now placed in the tribe Astereae. Cacosmia, described as new in the work, was placed in the section Helianthaeae. Cassini (1819) reviewed the work of Kunth in detail and redistributed the genera into his previously established tribes. Andromachia was recognized as a synonym of Liabum and placed in the Vernonieae. Cacosmia was also placed in the Vernonieae with the comment, "Cacosmia est une vernoniée voisine de l'Andromachia!" Later Cassini (1825) recognized five sections in the Vernonieae with the first, the Liabeae containing Munnozia Ruiz & Pav., Liabum Adanson, Oligactis Cass. and Cacosmia Kunth.

The concepts of Cassini prevailed for fifty years but Bentham (1873) placed Liabum in a distinct subtribe of the tribe Senecionideae. He said, "Liabeae is a small subtribe characterized by its imbricate involucre and Vernonioid style" and he added, "It has been almost universally classed under Vernoniaceae on account of its style; but the yellow heterogamous usually radiate capitula as well as the habit are very foreign to that tribe, whilst there is much that connects it with Senecionideae. The opposite leaves, though not common in the latter tribe, are to be met with in Arnica, Haploestes, and Gynoxys; and the style is scarcely so far removed from that of Gynura as the latter from the ordinary truncate style of Senecio. The W.-Indian and Columbian genus Neurolaena, two species, admitted on all sides to be a Senecionid, is very nearly allied to Liabum, and, indeed, closely connected with it through Schistocarpha, a Mexican and Peruvian genus of four species, with the opposite leaves of Liabum and the paleaceous receptacle of Neurolaena." Bentham placed Cacosmia in a subtribe Jaunieae of the Helenioideae with the comment "There remain four genera,

which, on account of their involucreal bracts, imbricate in several rows, increasing from the outer to the inner, are anomalous in the Helenioideae, . . ."

The concepts of Bentham were followed by Hoffman (1894) and and as such by all subsequent treatments. The Bentham - Hoffman concept seems to have been based primarily on an erroneous belief that nothing with ray flowers and opposite leaves should be closely related to the Vernonieae and also on a very unnatural broad concept of the Senecioneae. The concept presented here recognizes Cassini's basic insight into the closest relationships of Liabum but also recognizes Bentham's wisdom in removing the group from the otherwise very natural and well defined tribe Vernonieae.

Liabeae, tribus nova Asteracearum. Folia opposita subtus plerumque albo-tomentosa. Capitula heterogama; squamae involucri multiseriatae; radii sine antheris; corollae flavae; thecae antherarum inferne distincte prolongatae, cellulis exothecialibus quadratis vel elongatis distincte pauce vel multo noduliferis, appendicibus planis non glanduliferis intus simplicibus; styli florum discoideorum in nectariis partim immersi, ramis oblongis vel linearibus extus valde hirsutis intus anguste vel late continue stigmaticis. Grana pollinis regulariter vel irregulariter spinulifera non reticulifera.

Genus typicum: Liabum Adanson

The two most basic structures reflecting relationships within the Asteraceae are the styles and the stamens. In both of these structures the Liabeae are closely related to the Vernonieae and comparatively remote from other tribes. The style of the disk flowers has hairs on the outer surface to below the base of the branches and has a stigmatic surface of completely fused lines running along the inner surface of the branches to the tip. Such a combination of style branch and stigmatic line structure is approached but not equalled by a few members of the Eupatorieae. The stamen has the functional thecae extending well below the level of attachment and usually completely overlapping the collar. The anther appendage is broad and flat without concavity or costa. Evidence for relationship can also be gained from the multiseriate graduated form of the involucre, the long narrow shape of the corolla lobes, the pappus with usually two distinct series, and the tendency for irregular spine positions on the pollen.

Actual placement of Liabum and Cacosmia in the Vernonieae seems unwise on the basis of present knowledge. The opposite leaves, the presence of rays, and the yellow color of the corollas noted by Bentham and Hoffman are very significant differences. The lack of reticulating ridges on the pollen grains is also very important. In addition, there are tendencies in the Liabeae toward longer exothecial cells with terminal thickenings, a form unknown in the Vernonieae, and the anther appendages are generally firmer and sometimes hollow in a manner

known elsewhere only in the Eupatorieae.

The relegation of Liabum in the Senecioneae was rather obviously unnatural. Separate observations to this effect had been mentioned to the senior author some years ago by both R.M. King and Jose Cuatrecasas. The observations of the latter were based on extensive detailed study of the compositae in general and the Senecioneae in particular, and the true relationships of Liabum and Cacosmia were as fully suspected by Dr. Cuatrecasas as they were by Cassini. In contrast, the basis of Bentham's placement of the genera in the Senecioneae and Helenieae seems weak, and the primary motive must have been to exclude the genera from the Vernonieae. In both cases the Vernonia-type multiseriate involucre has proved an embarrassment, the Helenieae and Senecioneae both being characterized by simpler involucre. Bentham's comparison of the Liabum style branch with that of Gynura showed no insight into the basic differences in the form and placement of the stigmatic lines and the development of stylar appendages in the Senecioneae. The Bentham concept washes out completely with the realization that neither Neuro-laena nor Schistocarpha which he considered intermediate are members of the Senecioneae. The true relationships of the latter are analyzed in a following paper of this series.

The relationship of Cacosmia with Liabum cannot be seriously questioned. The former does have generally smaller heads and the flowers lack a pappus, but there are no other consistent differences. The vegetative portions of the plants are essentially identical. The development of true ray flowers lacking anthers and with modified non-hirsute styles is the same in both genera. Corolla lobes completely lacking stomates as in Cacosmia are found in a large group of Liabum species. Short exothelial cells with thickenings on all walls as in Cacosmia are found in four species of Liabum.

The proper placement of the Liabeae is of undoubted significance to understanding the overall evolution of the Asteraceae. The removal from the Senecioneae further diminishes the already fading belief that the tribe might be the oldest and most diverse in the family. The realization that two genera with fully differentiated rays are closely related to the Vernonieae is obviously important in evaluating the relative position of that tribe.

We wish to acknowledge R. M. King for calling special attention to some of the pertinent references of Cassini and Bentham.

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